THE SEX-RATIO IN THE WILD ANIMAL POPULATIONS OF THE NEW HEBRIDES.

By A. J. Marshall and John R. Baker, D.Sc.

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The chief biological object of the Oxford University Expedition to the New Hebrides (1933–4) was the study of the breeding seasons of animals in a remarkably unvarying climate, but we kept a careful record of all specimens obtained with a view to reporting on the sex-ratio. Our collections were made chiefly in eastern Espiritu Santo, though specimens were also taken in the west and in the small island of Gaua. We soon noticed that the great majority of our vertebrates showed a remarkable preponderance of males. The same peculiarity is shown by the natives of the islands, and those of the district called Sakau have one of the highest sex-ratios of any people in the world (see Baker, 1928).*

In this paper we report on the birds and mammals. The sex-ratio is given as the percentage of males, and the standard error of the ratio has been calculated from the formula $\sqrt{\frac{mf}{n}}$, where m is the percentage of males, f that of females, and n the total number of specimens counted.

The birds will be considered first.

All species of which we shot 40 or more specimens are considered in what follows. There are 20 such species and the total number of individuals shot of these species (of all ages) was 2,193. The sex-ratio of the whole group was 59 ± 1·0. Of the 20 species, only 3 had an excess of females, and in no case was such excess of females statistically significant. The highest sex-ratios were as follow:

Cacomantis pyrrophanus (cuckoo)	84 ± 4·9
Myzomela cardinalis (honey-eater)	81 ± 3·6
Rhipidura brenchleyi (flycatcher)	68 ± 5·8
Halcyon chloris (kingfisher)	67 ± 6·5
Turdus poliocephalus (blackbird)	65 ± 6·7

Of the total of 2,193 birds, 319 were juvenile. It is interesting to notice that the sex-ratio of the juveniles was as high (60 ± 2·7) as that of the adults (58 ± 1·1). We did not obtain any young *Cacomantis*, but in *Myzomela cardinalis* the sex-ratio of young was 78 ± 5·9 and of adults 83 ± 4·5. These figures show that high sex-ratio is not to any significant extent a product of differential mortality of the sexes in the later stages of growth.

The fact that sex-ratio is as high in young as in adults also shows that the preponderance of males is not due simply to the females being too much occupied with incubation to be shot. Other lines of evidence point in the same direction. Thus the highest sex-ratio of all (84 ± 4·9) is in a cuckoo, which does not incubate at all; and the flycatcher and kingfisher have high ratios, though in these families it is usual for both sexes to incubate. We do not think that our shooting was selective. Natives were nearly always paid the same price for specimens of each sex: when we were paying more for one sex, we neglected the birds received in our studies of sex-ratio. On the whole males have brighter plumage, but there is no direct correlation here with sex-ratio. Thus the male *Myzomela* is brilliantly-coloured and the female dull, and the species has a ratio of 81; but in *Cacomantis*, *Rhipidura brenchleyi*, and *Halcyon*,

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* We particularly wish to acknowledge our indebtedness to T. H. Harrison.

which also have very high sex-ratios, the sexes hardly differ externally. Further, in most of the species under consideration both sexes attend the nest and young. We do not think that bright plumage makes birds much easier to see, particularly under rain-forest conditions. A significant observation is that the young males of *Myzomela* are indistinguishable to the shooter from females, yet the sex-ratio of the young is just as high as that of the adults.

There appears to be some tendency for related birds to have similar sex-ratios. Thus two of the three birds which showed an excess of females were Campophagidae (both 49). The pigeons do not have very high ratios (59, 54, 53, 44). All three flycatchers have high ratios (68, 64, 62).

When the sex-ratio is very high, there must be much competition for hens. Most of the adult males of *Myzomela* have bare patches on their scarlet heads, presumably caused by fighting. This might suggest that a high ratio was of some benefit to the species, since the more virile males would breed and so a hardier stock might result. At the same time this does not mean that the sex-ratio is adaptive.

In addition to the shot birds reported upon above, we obtained and sexed 73 nestlings of the 20 species. It is unfortunate that the number was too small for a statistical study, but it is suggestive that 36 were males and 37 females. One is encouraged to think that the high sex-ratio of shot birds is caused by a greater mortality of females in the early days after leaving the nest.

Among the few mammals present in the islands we only collected enough specimens of two species for study of sex-ratio. These were the insectivorous bat, *Miniopteris australis*, and the large fruit-bat, *Pteropus geddiei*.

Miniopterus was collected by beating the air with sticks in the large cave in which it abounds. Only fully-grown specimens were obtained. It has a sharply-defined breeding season, during which the sex-ratio was found to be 66 ± 3·0; but it is clear that at this season the females avoid being killed, for in the long non-breeding season the ratio is 51 ± 1·9. We have here a species with approximate equality of the sexes.

In the fruit-bat the females retire to the depths of the forest when pregnant and are very difficult to obtain. It would be useless to try to estimate the sex-ratio at this time of the year. In the non-breeding season the females live socially with the males. We obtained specimens by shooting, and there is no question of differential shooting, for one cannot determine the sex until the animal has been shot. The sex-ratio, in the non-breeding season, is 69 ± 3·3. This includes some young ones, too few for separate statistical consideration.

It is difficult to believe that the high sex-ratio of New Hebridean animals could be adaptive, and indeed it seems probable that sex-ratio is seldom adaptive, except in those special cases in which male-producing sperms are eliminated in the testes (as in Aphids) or in which sex determination depends on whether the egg is or is not fertilized (as in aculeate Hymenoptera).

In most wild animals it appears that the sex-ratio is a matter of chance, with a tendency for the primary ratio to be near 50. It seems that in most mammals the male-producing sperms have some advantage in achieving fertilization (Crew, 1937), but there is no evidence that this is adaptive. Again, there is often differential death of the sexes, but here again there is no evidence that the primary sex-ratio is adapted to result in a ratio of value to the species. Differential mortality in a wild animal was strikingly demonstrated by Sasaki (1926). He found the sex-ratio of wild goldfish in Japan, lumping all specimens together, to be extraordinarily low, namely 11. Small specimens, 3–4 cm. long, showed a much higher ratio (32). There is clearly selective elimination of males during growth. Geiser (1924) has reported on the preponderance of females in the top-minnow, *Gambusia*, and has shown that there is nothing in spermatogenesis to account for it. As a rule the sex-ratio in marine Teleosts approaches equality, as Craigie (1927) has shown: this presumably indicates absence of differential mortality. In Elasmobranchs there is a tendency towards excess of females. In wild birds it is not rare to find an excess of males: thus Friedmann (1927) reports a sex-ratio of about 60 in three species of cow-bird (*Molothrus* and *Tangavius*).

It may be suggested that the ordinary chromosome mechanism of sex determination presents such advantages of simplicity as to outweigh any advantages which might accrue from adaptation of sex-ratio to the needs of the species. In those animals in which the male does not incubate eggs or protect female or young or territory, he is useless to the species except as a sort of dice-box for producing new combinations of genes in his sperms. It is difficult to believe that this function requires so many males as occur in most non-parthenogenetic species. Perhaps the Lamellibranch, *Teredo*, has adapted its sex-ratio to its requirements by somehow reducing the percentage of males to 0·2 (Pelseneer, 1906).

Summary.

There is a preponderance of males in the birds of the New Hebrides. It is argued that the sex-ratio is in general non-adaptive.

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AVES.

	Total No. shot.	Sex-ratio.
Columbae.		
Ptilinopus greyi	92	53 ± 5·2
Pt. tannensis	46	59 ± 7·2
Macropygia rufa	50	44 ± 7·0
Chalcophaps chrysochlora	81	54 ± 5·5
Coccyges.		
Cacomantis pyrrophanus	55	84 ± 4·9
Psittaci.		
Trichoglossus ornatus ..	419*	55 ± 2·4
Halcyones.		
Halcyon chloris	52	67 ± 6·5
Passeres.		
Rhipidura brenchleyi ..	65	68 ± 5·8
R. spilodera	69	62 ± 5·8
Passeres (contd.).		
Myiagra caledonica ..	42	64 ± 7·4
Coracina caledonica ..	80	49 ± 5·6
Neolalage banksiana ..	74	49 ± 5·8
Turdus poliocephalus ..	51	65 ± 6·7
Artamus leucorhynchus	54	54 ± 6·8
Pachycephala pectoralis	396	60 ± 2·5
Clytorhynchus pachycephaloides	99	56 ± 5·0
Zosterops lateralis	153	57 ± 4·0
Z. flavifrons	112	54 ± 4·7
Myzomela cardinalis ..	120	81 ± 3·6
Aplonis zeylanica	83	51 ± 5·5
All the above species together	2193	59 ± 1·0

MAMMALIA.

	Total No. shot.	Sex-ratio.
Cheiroptera.		
Miniopterus australis†‡ ..	716	51 ± 1·9
Pteropus geddiei†	201	69 ± 3·3

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* 48 specimens of unstated age not included.

† In non-breeding season.

‡ Killed with sticks.